

**Rainfall, Resources, and Dispersal in Southern  
Populations of *Euphydryas editha*  
(Lepidoptera: Nymphalidae)**

RO-4-122

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While the dispersal capacity of an insect species probably changes little from one generation to another, its actual dispersal or vagility may vary considerably. This is well documented for insects which have migratory generations, such as locusts, aphids, and butterflies, but remains virtually undocumented in non-migratory species. One exception is the butterfly, *Euphydryas editha*. Individuals of this species were originally shown to be extremely sedentary (Ehrlich, 1965), but in some populations the mean dispersal distance of individuals was recently observed to change dramatically from one generation to the next. These changes in vagility appeared to be influenced by the availability of oviposition plants and adult nectar resources; significantly greater vagility occurred in drier years when those resources were sparse (White and Levin, 1981).

However, subsequent field observations of four *E. editha* populations in Southern California indicate that the determinants of vagility are more complicated. In 1977 these populations exploded in size and mass dispersal was observed. Here we discuss how weather and butterfly population size interact to determine host plant availability and butterfly population dynamics. Additionally, we consider the biogeographic and genetic consequences of dramatic population fluctuations in *E. editha*, and the mechanisms by which both the butterflies and their host plants respond to environmental stress.

LIFE HISTORY

*Euphydryas editha* populations in San Diego County usually fly in a four to eight week period, starting as early as mid-January and ending as late as the end of April, depending on the timing of winter rainfall. Eggs hatch about ten days after oviposition and about two weeks later larvae enter an obligatory fourth instar diapause. Diapause terminates after winter rainfall when larval host plants are again available. Postdiapause larvae then feed through another four instars, pupate, and emerge as adults to complete the life cycle. The temporal proximity of the postdiapause larval feeding period to the oviposition and prediapause larval feeding periods is key to understanding year-to-year changes in host plant densities and in butterfly dispersal.

OBSERVATIONS

During the spring of 1977 rainfall preceding the flight of *E. editha* in the mesa grasslands of San Diego County and northern Baja California was just above the long-term average (11.48 cm versus average 11.15 cm, November-January; NOAA

Climatological Data). Based on the hypothesis that normal rainfall would provide adequate plant resources, we predicted limited adult butterfly movements. Instead, in an early and extended flight period, February through April, colonies exhibited local population explosions and very high rates of dispersal. Several San Diego area populations studied by our group for almost a decade (Ehrlich et al., 1975; Singer and Ehrlich, 1979) increased nearly two orders of magnitude, to hundreds of thousands of individuals at each of four population centers: Lower Otay (LO), Upper Otay (UO), Brown's Field (BF) on Otay Mesa, and La Pressa Rodriguez (LPR) near Tijuana.

Although butterflies were extremely abundant, there was no apparent scarcity of nectar. Flowers most commonly visited (*Eriogonum fasciculatum* Benth, *Vigueria laciniata* Gray, *Linanthus dianthiflorus* (Benth) Greene, and *Dichelostemma pulchellum* Heller) were available in large numbers. Thus, adult movements induced by a lack of proximate nectar sources, such as those observed by Gilbert and Singer (1973), seemed unlikely. However, the larval host plants, *Plantago insularis* Eastwood and *P. hookeriana* F. and M., were scarce or absent. Nearly eight hours spent searching for these normally abundant plants resulted in only a few dozen being found at UO and BF, and none at either LPR or LO. On the basis of this search we estimate that the portion of the plant crop consumed by postdiapause larvae was more than 99%, considerably higher than the maximum of 80% previously reported (White, 1974). Defoliation of this degree results in significant larval starvation and competition for host plant resources. Nonetheless, enough food was apparently available to allow emergence of very large numbers of adults. The very nearly total defoliation of larval host plants produced a scarcity of oviposition sites, and this elicited movements far in excess of any previously recorded for either sex (White and Levin, 1981). Egg-laden females were captured several kilometers north of LO and UO in unsuitable chaparral habitat and similar distances west, over barley fields and other inappropriate habitats lacking host plants. At LO the flight observed of both sexes was directional, away from the population centers described by White and Levin (1981).

#### DETERMINANTS OF VAGILITY

Given these latest observations, we can now attempt a more comprehensive model to explain generation-to-generation changes in vagility in this species. Figure 1 illustrates how factors acting on butterfly host plants determine adult population dynamics. Dry winters result in adult *Euphydryas editha* that exhibit increased vagility, because: 1) nectar plant quantity and quality are locally reduced, 2) fewer suitable oviposition plants are available and these senesce earlier, so females must fly farther to oviposit, and 3) postdiapause larvae defoliate many of these plants before adult females emerge to oviposit. When a wet year is followed by a dry year dispersal is intensified; and, the greater the difference in rainfall from one year to the next, the greater the change in dispersal. This is because the larger the difference in rainfall, the greater will be the imbalance in the densities of the emerging adult population and the available oviposition plants. When defoliation by postdiapause larvae is particularly extreme, competition for limited oviposition plants may become intense for those individuals who become adults. In the more usual course of events, however, postdiapause larval starvation is

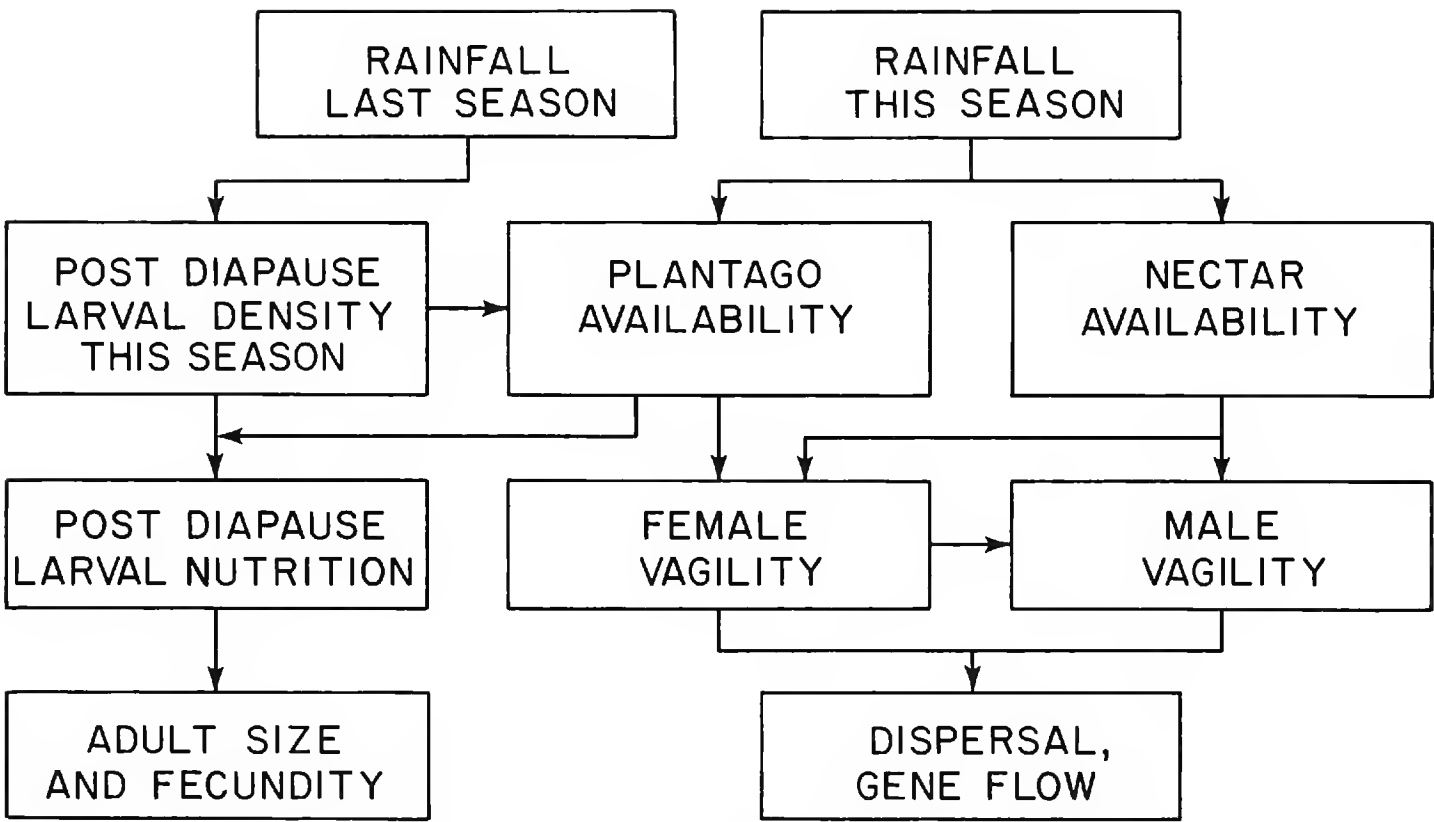


Figure 1. Flow chart of the influence of rainfall on host plant availability, larval survival, fecundity of adults, and gene flow. Discussion in text.

minimal, adult resources and oviposition plants are abundant, and adults are sedentary (this is what White and Levin observed in 1973).

Even without a decline in rainfall, consecutive years of average or better rainfall apparently result in such large population build-ups that postdiapause larvae almost totally defoliate the *Plantago* crop regardless of its abundance. This is what seems to have occurred in 1977. Whether larval food-stress predisposes adults to migrate is not known, but the presence of nectar appears not to inhibit emigration under these circumstances. These populations of butterflies are thus regulated by rainfall (which determines plant crop density) in a largely density-independent manner most years. But, intermittent generations are subject to severe competition, hence are regulated in a density-dependent manner.

ADAPTATIONS TO STRESS IN PLANTS AND BUTTERFLIES

The long-term status of larger local populations of *Plantago* and *Euphydryas* in Southern California appears to be little affected by host plant defoliation, larval starvation, and adult dispersal. Though we observed essentially total defoliation of *Plantago* in 1977, so that no seed was set, the autumn rains that year produced large standing crops from the seed bank remaining in the soil from previous years. In February of 1978, an average of 19 plants per square decimeter were counted in 15 randomly selected plots (range: 0–67) at LO. We have observed similar phenomena in Northern California where *Euphydryas* use annual larval host plants, which nearly disappeared due to drought rather than to defoliation, forcing small *E. editha* populations to extinction (Ehrlich et al., 1980).

Three characteristics of *Euphydryas editha*, particularly well developed in the *wrighti* subspecies, seem to be key to its survival in this relatively unpredictable environment. First, adult size shows a positive correlation with rainfall and is



greatest when rainfall-dependent host plant density and quality are high (White and Levin, 1981; Murphy et al., in prep.). In seasons of poor host plant conditions, larvae pupate small, rather than feeding to some "optimum" size. Though smaller adult females produce fewer eggs in such years, offspring are provided sufficient time to reach diapause before host plants senesce. Second, postdiapause larvae experiencing food-stress have been observed to re-enter diapause (Singer and Ehrlich, 1979). This may explain why in 1978 the adult population was of moderate size: larvae from 1976 re-entered diapause in 1977 to emerge successfully in 1978. Third, emergence from diapause may be controlled more by rainfall and host plant availability than by time of year, and appears to be less obligatory than in other subspecies such as Northern California's *E. editha bayensis*. Abundant host plant crops are used whenever available, even when they occur out of season due to unusual rainfall. The sizes of fall-flying generations, such as the one reported for November 1936, may resemble those of normal February–March generations (Fred Thorne, pers. comm.). The pool of diapausing larvae is thus replenished whenever rainfall is substantial, rather than only in years with good winter rainfall.

#### BIOGEOGRAPHIC AND GENETIC CONSEQUENCES OF MASS DISPERSAL

Clearly important in the immigration-extinction dynamics of Southern California *Euphydryas editha* is the role of migrants moving into unoccupied sites during these infrequent population explosions. Populations of *E. e. wrighti* have long been known to vanish for years, then to suddenly reappear (Orsak, 1977; J. W. Johnson, pers. comm.). We suspect that in many years rainfall, and therefore host plants, are insufficient to support populations in many small, topographically homogeneous or otherwise marginal habitats and that local population extinction is likely common there. Between population outbreaks, populations may survive only in the largest, most diverse habitats. During consecutive years of adequate rainfall these populations increase in size and exhaust host plant availability which leads to mass dispersal. Larger populations then act as sources of migrants to uninhabited areas, which due to adequate rainfall in these years support sufficient plant resources to make establishment or re-establishment of populations possible. The largest, most persistent populations thus support the long-term existence of many other populations.

This extinction/recolonization dynamic has implications for conservation efforts aimed at this species (Murphy and Ehrlich, 1980). (The *wrighti* subspecies has been placed on several review lists for potential endangered status.) The extirpation of a single, large reservoir population of *wrighti* may effectively deny other habitats necessary migrants, creating a ripple effect of irreversible long-term extinctions. We suspect that just such a circumstance has eliminated *Euphydryas editha wrighti* from Orange County and much of coastal San Diego County, and now threatens populations in Riverside and inland San Diego Counties in California.

The role of infrequent episodes of mass dispersal in affecting gene flow between *Euphydryas editha* populations is not so clear. There is a lack of any significant genetic difference among populations at UO, LO, and BF (McKechnie et al., 1975; C. E. Holdren, pers. comm.). In most years the migration rates among these populations seem to be very low, probably less than that necessary to keep the frequencies of selectively neutral alleles the same (Lewontin, 1974). It is tempting,

therefore, to ascribe the observed genetic similarities to population explosions of the sort seen in 1977. However, the environmental conditions that result in increased dispersal make reproduction nearly impossible for migrants arriving at occupied population sites. Hence, while adult movements are necessary for gene flow to occur, they are not equivalent to gene flow in the case of established populations.

### CONCLUSIONS

After extensive study of several populations of *Euphydryas*, movement patterns appeared to be characteristic of local populations and determined by local resource distribution (Gilbert and Singer, 1973). Further research showed that for one population, year-to-year changes in rainfall produce changes in resource availability, which in turn result in changes in vagility (White and Levin, 1981). Our current understanding contains an additional element: prior build-up of insect population numbers may cause resource depletion resulting in host plant scarcity even in years of favorable weather. Thus the dynamic history of a population can have a significant effect on dispersal patterns of its individuals, and on the overall distribution of the organism.

### ACKNOWLEDGMENTS

We gratefully acknowledge support by a series of grants from the National Science Foundation to Paul R. Ehrlich, including DEB78-22413. D. D. Murphy is presently supported by a grant from the Koret Foundation of San Francisco. Bruce A. Wilcox, Paul R. Ehrlich, M. Deane Bowers, and two reviewers commented on drafts of this manuscript. Secretarial support was provided by Old Dominion University, Norfolk, Virginia.

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